

PERSPECTIVES ON THE ORIGIN OF THE FLORISTIC
SIMILARITY BETWEEN EASTERN ASIA AND
EASTERN NORTH AMERICA¹

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THE FLORISTIC SIMILARITY between eastern Asia and eastern North America has been recognized since the time of Linnaeus (see Graham, 1972a; Boufford & Spongberg, 1983) and was emphasized through the work of Asa Gray (1840, 1859). Scientific study of this pattern has continued, and its importance in current botanical thought is shown by the several symposia recently convened on the topic, most notably those at the XI International Botanical Congress in Seattle and the Japanese-American meeting in Corvallis in 1969 (Graham, 1972b), at the Missouri Botanical Garden in 1982, and at the Japanese-American conference held at the Cary Arboretum of the New York Botanical Garden in 1983.

In general, presentations at these conferences have followed one of three approaches: enumeration of taxa exhibiting this pattern; discussion of some aspect of the biology (e.g., anatomy, ecology, cytology, chemistry) of a taxon or taxa exhibiting this pattern; or examination of the paleontological aspects of this question, involving postulated routes of movement or changes over time in one geographic area. However, two major questions have never been directly addressed and have only rarely been alluded to in these symposia: first, is the pattern of similarity between eastern Asia and eastern North America real, and second, if it is, what are all the possible ways by which the pattern might have arisen?

A proper solution to the first question requires a rigorous examination of the patterns of similarity between eastern Asia and eastern North America in light of the larger biogeography of the Northern Hemisphere. In particular, "three-area" tests of the variety suggested by cladistic biogeographers need to be made and analyzed to determine whether the eastern Asian-eastern North American similarity is a unique pattern or simply a distinctive subset of a larger pattern. From a paleontological perspective, I suspect that the latter is both the more correct assumption and the better working hypothesis. I believe that this conclusion is also inherent in reviews of modern angiosperm biogeography (e.g., Thorne, 1972). However, it is the second of the two questions that I wish to explore in depth here, as it places the following paper (Tiffney,

¹This is the first of two related papers. The second, entitled "The Eocene North Atlantic Land Bridge: Its Importance in Tertiary and Modern Phytogeography of the Northern Hemisphere," will be published in the April, 1985, issue of the *Journal of the Arnold Arboretum*.

1985) on the importance of early Tertiary North Atlantic land bridges in the historical context of all possible origins of the eastern Asian–eastern North American floristic similarity. For this purpose I will assume that the pattern is “real”; I do not think that this assumption biases the inquiry into its origins.

The purpose of this paper is to call attention to the diverse historical components of this biogeographic pattern and to emphasize that it did not arise as a result of a single historical event. Scientists working with this problem recognize that it is complex but have not presented a logical explanation of its components. A clear exposition of the range of biogeographic factors involved in the origin of the eastern North American—eastern Asian floristic similarity would make it possible to evaluate the individual histories of plant taxa that contribute to the pattern. This information should in turn enhance our knowledge of other aspects of the biology of the plants under investigation. As a general survey, this paper may prove wrong in its particulars but will provide a starting point for an examination of the variables involved.

PATTERNS AND PROCESSES

The origin of the floristic similarity of eastern Asia and eastern North America involves an interplay of three factors: changing geography, changing climate, and evolving (both phylogenetically and ecologically) biota. The last factor is not completely independent of the former two, as physical events are important in both allopatric speciation and natural selection.

Before the interaction of these three factors and the range of possible ways by which the eastern Asian–eastern North American similarity arose can be discussed, three other biogeographic questions must be considered: the concept of a “center of origin” of the flora that now displays this distribution pattern, the nature of past plant movements in general (specifically, the distinction between the dispersal of “floras” and “individuals”), and the biogeographic history of herbaceous angiosperms. These topics have had a strong influence, whether perceived or not, on thought concerning the origin of the eastern Asian–eastern North American floristic pattern.

ELEMENTS OF PALEOPHYTOGEOGRAPHY

CENTERS OF ORIGIN AND ASSOCIATED PROBLEMS

The similarity of the extant floras of eastern Asia and eastern North America arose through movements of taxa in the geologic past. Gray (1878), considering the geographic arrangement of the Northern Hemisphere, proposed that the pattern developed due to a glacially induced southward movement of an earlier thermophilic flora with a polar distribution. This perspective was developed by Chaney (1947) and refined by Axelrod (e.g., 1966) as the “geofloral hypothesis.” Subsequent workers have found no evidence of a Late Cretaceous/early Tertiary circum-Arctic flora similar to that of the temperate regions of eastern North America and eastern Asia today (see Hickey *et al.*, 1983; Hickey, pers. comm.).

Wolfe (1975, 1977) argued from paleobotanical evidence that the origin of the similarity of the floras of eastern Asia and eastern North America involved the evolution of a large number of modern taxa in the latest Cretaceous and early Tertiary. These first appeared in the mid-latitudes of the Northern Hemisphere and spread by existing land bridges, ultimately forming a relatively homogeneous early Tertiary flora. Both paleoclimatological data (Kennett, 1977; Buchardt, 1978; Collinson *et al.*, 1981) and the taxonomic composition of this early Tertiary flora demonstrate that early Tertiary climates were at least paratropical in the mid-latitudes of the Northern Hemisphere. For this reason, and to distinguish this assemblage from coeval floras in the Southern Hemisphere (Wolfe, pers. comm.), Wolfe (1975) referred to these newly evolved plants as forming a "boreotropical flora."

Wolfe (1975, 1977) did not cite a specific "center of origin" for the boreotropical flora, but certain aspects of its composition and distribution have been taken to suggest such a center. The greatest diversity of modern taxa derived from this early Tertiary flora is now found in eastern Asia. Similarly, the affinities of many fossil representatives of the boreotropical flora found in Europe and North America lie with extant taxa found in Japan, China, northern India, Indomalaysia, and some western Pacific islands. These include plants of temperate, subtropical, and tropical environments. Further, the modern eastern Asian flora includes a host of taxa that are presumed to be phylogenetically primitive, with many occurring as monotypic families or genera (Wang, 1961).

These factors all lead to the common perception that southeastern Asia was the evolutionary source area both of the angiosperms as a whole and of the modern flora of the Northern Hemisphere (e.g., Takhtajan, 1969; Smith, 1970). The interpretation of southeastern Asia as the place of origin of the angiosperms has been rejected in recent years (e.g., Raven & Axelrod, 1974), and its role as the sole source for the boreotropical flora similarly disintegrates under scrutiny. In both cases the alternative interpretation that southeastern Asia was a great refugium or "museum" appears to be correct. Perhaps more importantly, the dismissal of this "center of origin" should not imply the necessity of locating a new one. I agree with Wolfe (1975) that the boreotropical flora probably had a diffuse origin involving several areas of the Northern Hemisphere. Evaluation of the status of southeastern Asia, and of the latter suggestion, requires an examination of what distinguishes southeastern Asia from other areas of the Northern Hemisphere in the past and the present, as well as of what evidence exists for other places of origin of the boreotropical flora. The latter further requires the distinction between a localized center of origin and a diffuse origin of this flora.

Little paleobotanical evidence is available for southeastern Asia in the early Tertiary. Guo (1980) and Hsü (1983) have reviewed evidence of the Late Cretaceous and Tertiary flora and vegetation of China. Although Hsü includes some palynological data, generally at the family level, both reviews are largely dependent on evidence from fossil leaves. Hickey (1973) and Wolfe (see Hickey & Wolfe, 1975) have indicated that many existing identifications of fossil leaves are erroneous and in need of revision. Thus, the composition of these Chinese

floras is unclear. Muller's (1968) report on early Tertiary palynology of Borneo indicates that several typical elements of the modern flora did not arrive at the sample site until after the Eocene. This suggests that the extant flora of this area developed through the Tertiary and is not the product of a single, local, early Tertiary origin. Vertebrate evidence (Li & Ting, in press; see also McKenna, 1983b) indicates that the Chinese Paleocene fauna was distinct from that of the rest of the Northern Hemisphere; the same may have been true of its early Tertiary flora. Circumstantial evidence further suggests that southeastern Asia is well suited to preserve taxa of tropical to warm-temperate affinity. During the early to middle Tertiary, it was linked with central Asia and Europe by the Tethys Seaway (see Tiffney, 1985, *map 6*), and to western North America via the Bering land bridge. Southeastern Asia is topographically diverse and was presumably equally so in the later Tertiary, encompassing a wide range of habitats and climates. Further, it was and is protected from invasion of Arctic air masses by east-west oriented mountains that had sufficient gaps to permit the southward movement of plants from the north. In short, southeastern Asia could be expected to serve as a refugium for thermophilic plants in an ice age.

With respect to the second question, the other possible areas of origin of the boreotropical flora involve the Late Cretaceous-early Tertiary low latitudes, high latitudes, and mid-latitudes of the Northern Hemisphere. No real data are available on plant evolution in the tropics at this time; this is one of the challenges to angiosperm paleobotany. Recent evidence (Hickey, 1981a; Hickey *et al.*, 1983; Hickey, pers. comm.) from high latitudes indicates the presence of a species-poor, deciduous flora. Although several components of this flora (e.g., *Betula* L., *Cercidiphyllum* Sieb. & Zucc., *Metasequoia* Miki, Juglandaceae) are members of the boreotropical flora, the latter unit did not evolve here.

For the mid-latitudes the evidence is less direct, but suggestive. In the Late Cretaceous, palynological data indicate that the Northern Hemisphere was broadly divided into two primary floristic provinces: the *Aquillapollenites* Rouse province of western North America and eastern Asia, and the *Normapolles* province of eastern North America and Europe (Muller, 1970; Srivastava, 1981), which reflect the geography of the time—eastern Asia and western North America were linked by the Bering land bridge, and eastern North America and Europe were linked by a North Atlantic land bridge. Separated by the Turgai Straits and other seaways through central Asia and eastern Europe (Vinogradov, 1967–1968; see Tiffney, 1985), and by the Midcontinental Seaway through central North America, these provinces disintegrated at the end of the Cretaceous (Muller, 1970), shortly before the rise of the boreotropical flora. With their different floristic compositions, they each probably contributed distinctive elements to the succeeding boreotropical flora.

The paleogeography of the early Tertiary also suggests other possible mid-latitude sources of the boreotropical flora. In particular, the island chains of the European and Middle Eastern portions of the Tethys Seaway seem likely to have been excellent sources for the evolution of new taxa through allopatric speciation. The great longitudinal span of the Tethys, from eastern Asia to Europe and west at least as far as Caribbean North America, may have provided a natural route for taxa that evolved in a limited area of the seaway. Certainly

both classic boreotropical floras (e.g., the London Clay Flora of England (Reid & Chandler, 1933; Chandler, 1964), the Geiseltal Flora of Germany (Mai, 1976), the Haselbach Flora of Germany (Mai & Walther, 1978), the Burgas Flora of Bulgaria (Palamarev, 1973), the Clarno Flora of Oregon (Scott, 1954; Chandler, 1964; Manchester, 1981a, 1983)) and modern refugia rich in boreotropical elements (Central America, southeastern North America, the Caucasus, the Himalayas, southeastern Asia) lie along the ancestral path of the Tethys. Other mid-latitude areas of the early Tertiary may also have provided the geographic diversity necessary for allopatric speciation. In North America the early Tertiary rise of the Rocky Mountains resulted in an increasingly diverse landscape and was associated with many floristic changes (Leopold & MacGinitie, 1972), which probably involved the evolution of new taxa *in situ* rather than their movement in from other areas.

In summary, no paleontological evidence exists to support the concept of eastern Asia as the sole center of origin of the modern flora of the Northern Hemisphere. A limited number of boreotropical taxa have been recognized in the early Tertiary of the Arctic; geographic considerations suggest that other areas in the mid-latitudes of the early Tertiary could well have served as diffuse centers of origin and speciation. Resolution of the sources of the boreotropical flora will require careful analysis of the geographic history of its specific component lineages (e.g., Manchester's (1981b) survey of the Juglandaceae).

THE BALANCE OF FLORAS AND INDIVIDUALS IN "MIGRATION"

Discussion of the origin of the modern flora of the Northern Hemisphere invariably entails consideration of the "migration" of ancestral communities or floras. This idea can be traced to Darwin (1859) and Gray (1878). However, the first modern concepts of the community can be ascribed to the ecological work of Clements (1916, 1928), who considered the community to be the basic structural unit of the earth's vegetation. He regarded individual communities as tightly interdependent groupings of plants united through adaptation to a particular climate and environment and having almost organismlike emergent properties. Clements argued his case cogently, and his ideas had a strong influence on American botany for many years. One of those influenced was R. W. Chaney, who saw in this approach an ecological explanation to patterns observed in the fossil record. From this arose the geofloral concept—the hypothesis that past phytogeographic changes involved the movement of monolithic "climax" communities of set taxonomic composition across the face of the earth in response to climatic stimuli (Chaney, 1947). In particular, he believed that the present similarity of the floras of eastern Asia and eastern North America resulted from the early Tertiary southward movement from a polar source of a temperate "Arcto-Tertiary Geoflora" of modern floristic and vegetational composition. Viewed in the context of contemporary science, this was an up-to-date, biological explanation of the observed facts.

However, the Clementsian concept of the community as a monolithic unit was not without its detractors. In particular, H. A. Gleason (1926) countered the community concept of plant ecology with what he termed the "indivi-

dualistic concept." Gleason contended that plant species acted independently, that range expansions and contractions occurred on the level of individual organisms, and that the "communities" of Clements were nothing more than chance aggregations of species sharing some common physiological requirements and tolerances. In some senses the individualistic approach is the dominant perspective in modern community ecology, as reflected both in Whittaker's concept of gradients (1967) and in the general sense that Clementsian "climax" communities do not exist.

The paradox of the Clementsian-Gleasonian debate is that both sides are right. Communities do not move in lockstep, but neither are plant groupings totally completely random associations of species. Davis (1976, 1981) has demonstrated that several taxa that are found together in portions of the modern temperate deciduous forest of eastern North America moved into these communities after the Pleistocene from different refugial sources and following different routes of dispersal. However, although plants disperse as individuals, different taxa may be constrained by similar environmental factors such as moisture, temperature, soils, or dispersal agents in such a way that "communities" of mutual tolerance are maintained as loose but recognizable units. With the loss of resolution dictated by the nature of the fossil record, it is not surprising that paleontologists perceive a pattern involving "floras" rather than individuals. The danger lies in accepting this perception at face value without seeking the dynamic biological factors that underlie it.

The critical response to the geofloral hypothesis has not necessarily followed the community-individual debate, but elements of that discussion are present. Wolfe (1969, 1975, 1977) surveyed the fossil record and found no evidence of a polar Arcto-Tertiary Geoflora, or of phytogeographic evolution of the Northern Hemisphere involving the mass movement of unit floras. However, he has demonstrated the early Tertiary appearance of a floristic unit that he termed the "boreotropical flora." Although Wolfe never envisioned this flora as uniform in its composition, its name conveys the impression that it was fairly homogeneous. This raises conceptual problems, as it might appear that the sole difference between the Arcto-Tertiary Geoflora and the boreotropical flora is that the latter did not "migrate" but simply appeared. In a sense this is true, but the real distinction between the two lies in their internal dynamics. The geofloral hypothesis assumed a stable community with a static composition; the boreotropical flora concept, a constant internal flux of taxonomic composition, both in its origin and during its existence. Thus, the boreotropical flora is envisioned not as sweeping out from a single source but as rapidly accumulating through the dispersal of separately derived taxa into common areas. Although the reason for the initial appearance of so many boreotropical taxa during the early Tertiary is unclear (but see Tiffney, in press, for a possible explanation), the unique proximity of Northern Hemisphere continents in the early Tertiary, together with the warm climates of that time, explains their rapid spread. Similarly, after its establishment the boreotropical flora probably displayed considerable internal variation. I suspect that during the times of maximum land connection in the Northern Hemisphere, although the flora was characterized by a few distinctive taxa that were known from all or most

of the range of the flora (e.g., *Nypa* Steck, Icacinaceae, Mastixiaceae), individual species generally occupied only a portion of the range at any one time. As time progressed and climate and geography altered, this level of variation gave way to allopatric speciation and increased local differentiation.

Finally, some word is appropriate regarding one antithesis of floral “migration”—the hypothesis that the floristic similarity of eastern North America arose largely through chance long-distance dispersal (e.g., Iltis, 1982, 1983). This hypothesis is at odds with paleobotanical evidence for the existence of a boreotropical flora. Further, biotas resulting from long-distance dispersal are often dysharmonic; that is, they contain an imbalance of ecological constituents (Carlquist, 1974). The floras (and faunas) of eastern Asia and eastern North America contain a diverse array of constituents and could not have resulted entirely or in large part from the effects of long-distance dispersal. Finally, while long-distance dispersal is significant in explaining the past and present distribution of individual taxa, it is a counterproductive and anarchic hypothesis when used to explain patterns involving entire biotas. A dispersal hypothesis eliminates the ability to make predictive hypotheses and reduces the science of biogeography to chance.

THE DIFFERENTIAL APPEARANCE OF TAXA

Analogous to simplistic models of “single centers of origin” and “migration of unit floras” is the all-too-human tendency to seek a single time for the origin of the similarity of the floras of eastern Asia and eastern North America. Although Wolfe’s boreotropical-flora model of the early Tertiary provides much to explain the extant phytogeography of the Northern Hemisphere, I believe that it has given the unintended impression that the eastern Asian–eastern North American similarity is a function of a single time-limited historical event. However, analyses of phytogeographic patterns reveal that the individual taxa involved appeared in the fossil record at different times (which may reflect their evolution at different times), have different ecological adaptations, particularly as reflected in physiognomy, and are presently adapted to different climatic regimes. In short, the observed similarity of the two modern floras involves a range of taxa with rather different histories, habitats, and habits. This suggests that the similarity did not arise as the result of a single past event. Closer examination of the fossil record supports this contention. I will look at three particular aspects: the time of origin of specific families; the time of origin of herbaceous angiosperms, many of which are included in this pattern; and the nature of the different climatic tolerances of taxa constituting the modern eastern Asian–eastern North American pattern.

ORIGINS AND AFFINITIES. Some of the plants now having an eastern Asian–eastern North American distribution pattern belong to families that appeared in the fossil record at different times in the Tertiary. As a sample of the plants now showing this geographic pattern, I take those described in the classic work of H. L. Li (1952, 1972) and those mentioned by participants in the symposium that prompted the present paper, together with a few assembled from other sources (see TABLE 1). For the first occurrences of modern families in the fossil

TABLE 1. Age of origin of some families held in common between the floras of eastern Asia and eastern North America.

REPRESENTATIVE				
FAMILY ^a	GENERA ^b	REFER- ENCE ^c	POLLEN DATE ^d	FRUIT AND SEED DATE ^e
Aquifoliaceae	<i>Ilex</i> L.	5	Turonian	Paleocene
Buxaceae	<i>Pachysandra</i> Mi- chaux	4	Campanian	Mid-Miocene
Juglandaceae	<i>Carya</i> Nutt.	4	Campanian	Paleocene
Leguminosae	<i>Gymnocladus</i> Lam., <i>Cladras- tis</i> Raf., <i>Wiste- ria</i> Nutt., <i>Apios</i> Medikus	4	Maastrichtian	Paleocene
Symplocaceae	<i>Symplocos</i> Jacq.	5	Maastrichtian	Early Eocene
Theaceae	<i>Gordonia</i> Ellis, <i>Stewartia</i> L.	4	Early Eocene	Late Cretaceous
Aceraceae	<i>Acer</i> L.	5	Oligocene	Paleocene
Anacardiaceae	<i>Rhus</i> L.	5	Paleocene	Early Eocene
Araliaceae	<i>Panax</i> L.	4	Paleocene	Mid-Eocene
Caprifoliaceae	<i>Triosteum</i> L., <i>Diervilla</i> Miller, <i>Weigela</i> Thunb.	4	Mid-Eocene	Paleocene
Cyperaceae	<i>Carex</i> L., <i>Schoe- noplectus</i> (Reichb.) Palla	3	Mid-Eocene	Paleocene
Hamamelidaceae	<i>Hamamelis</i> L.	4	Paleocene	Early Eocene
Nyssaceae	<i>Nyssa</i> Gronov. ex L.	4	Paleocene	Early Eocene
Polygonaceae	<i>Antenoron</i> Raf., <i>Polygonum</i> L.	4, 5	Paleocene	Late Eocene
Rosaceae	<i>Rhodotypos</i> Sieb. & Zucc., <i>Kerria</i> DC., <i>Neviusia</i> A. Gray	4	Oligocene	Paleocene
Lauraceae	<i>Sassafras</i> Trew, <i>Lindera</i> Thunb.	4	Paleocene	Late Paleocene
Ericaceae	<i>Pieris</i> D. Don, <i>Lyonia</i> Nutt., <i>Epigaea</i> L.	4	Pliocene	Late Paleocene
Rutaceae	<i>Zanthoxylum</i> L.	5	Pliocene ^f	Late Paleocene
Vitaceae	<i>Vitis</i> L., <i>Partheno- cissus</i> Planchon	5, 11	Oligocene	Late Paleocene
Araceae	<i>Symplocarpus</i> Salisb.	4	Late Miocene	Early Eocene
Celastraceae	<i>Celastrus</i> L.	5	Oligocene	Early Eocene
Cornaceae	<i>Cornus</i> L.	6	No data	Early Eocene
Ebenaceae	<i>Diospyros</i> L.	5	Early Eocene	Early Eocene
Magnoliaceae	<i>Liriodendron</i> L., <i>Magnolia</i> L.	4	Mid-Eocene	Early Eocene

TABLE 1 (continued).

REPRESENTATIVE				
FAMILY ^a	GENERA ^b	REFER- ENCE ^c	POLLEN DATE ^d	FRUIT AND SEED DATE ^e
Menispermaceae	<i>Menispermum</i> L.	4	No data	Early Eocene
Santalaceae	<i>Buckleya</i> Torrey, <i>Pyrularia</i> Mi- chaux	4	Early Eocene	Mid-Eocene
Staphyleaceae	<i>Staphylea</i> L.	11	Pliocene	Early Eocene
Styracaceae	<i>Halesia</i> J. Ellis ex L., <i>Styrax</i> L.	4, 5	No data	Early Eocene
Umbelliferae	<i>Sanicula</i> L.	5	Early Eocene	Mid-Miocene
Bignoniaceae	<i>Campsis</i> Lour., <i>Catalpa</i> Scop.	4	Mid-Eocene	Mid-Eocene
Oleaceae	<i>Chionanthus</i> L.	4	Oligocene	Mid-Eocene
Rubiaceae	<i>Mitchella</i> L., <i>Gali- um</i> L.	4, 7	Late Eocene	Mid-Eocene
Acanthaceae	<i>Justicia</i> L., <i>Diclip- tera</i> Juss.	11	Early Miocene	Late Eocene
Guttiferae	<i>Ascyrum</i> L.	4	No data	Late Eocene
Liliaceae	Tribe Helonieae	9	Late Eocene	No data
Ranunculaceae	<i>Trautvetteria</i> Fischer & Mey- er, and the closely related genera <i>Hydras- tis</i> Ellis ex L. (N. Am.) and <i>Glaucidium</i> Sieb. & Zucc. (E. Asia)	4	Early Miocene	Oligocene
Labiatae	<i>Stachys</i> L., <i>Aga- stache</i> Clayton, <i>Meehania</i> Brit- ton	11	Pliocene	Mid-Oligocene
Primulaceae	<i>Trientalis</i> L., <i>Sa- molus</i> L., <i>Lysi- machia</i> L.	11	Pliocene	Mid-Oligocene
Saururaceae	<i>Saururus</i> L.	4	No data	Mid-Oligocene
Compositae	19 genera in com- mon	2	Oligocene	Mid-Miocene
Verbenaceae	<i>Callicarpa</i> L., <i>Clerodendrum</i> L., <i>Vitex</i> L.	11	Early Miocene	No data
Loganiaceae	<i>Gelsemium</i> Juss.	4	No data	Mid-Miocene
Scrophulariaceae	<i>Veronicastrum</i> Moench	4	Mid-Miocene ^s	Mid-Miocene
Saxifragaceae	<i>Decumaria</i> L., <i>As- tilbe</i> Buch.- Ham., <i>Hydran- gea</i> L.	4	No data	Mid-Miocene

TABLE 1 (continued).

REPRESENTATIVE				
FAMILY ^a	GENERA ^b	REFER- ENCE ^c	POLLEN DATE ^d	FRUIT AND SEED DATE ^e
Berberidaceae	<i>Jeffersonia</i> Bartram, <i>Podophyllum</i> L., <i>Diphyleia</i> Michaux, <i>Caulophyllum</i> Michaux	4	No data	Late Miocene
Cruciferae	<i>Arabis</i> L., <i>Draba</i> L., <i>Cardamine</i> L.	11	Pliocene	Late Miocene
Crassulaceae	<i>Penthorum</i> Gronov. ex L.	4	No data	Quaternary
Phytolaccaceae	<i>Phytolacca</i> L.	10	No data	Quaternary

^aListed in order of age of appearance, then alphabetically when of similar age. Age of first appearance is determined from fossil records of pollen and of fruits and seeds; where the two differ, the older age is used to order the families.

^bRepresentative modern genera with an eastern Asian–eastern North American distribution pattern.

^cReference(s) to modern distribution pattern by number: 1) Constance, 1972; 2) H. Koyama, 1983; 3) T. Koyama, 1983; 4) H. L. Li, 1952; 5) H. L. Li, 1972; 6) Sharp, 1972; 7) Shimizu, 1983; 8) Tamura, 1983; 9) Utech, 1983; 10) Wada & Ihara, 1983; 11) personal data.

^dEarliest date recorded for family, based on pollen records (Muller, 1981). Stratigraphy according to individual author’s citations, arranged after Van Eysinga (1975).

^eEarliest date recorded for family, based on fruit and seed records (B. H. Tiffney, unpubl. data). Stratigraphy according to individual author’s citations, arranged after Van Eysinga (1975).

^fTraverse (1955) reported pollen of the Rutaceae from the Brandon Lignite of Vermont (Oligocene?).

^gMuller indicates (1981) that some Paleocene pollen may ultimately prove to have affinities with the Scrophulariaceae.

record, I refer to Muller’s (1981) compilation of the palynological record and to similar unpublished data of my own on fossil fruits and seeds. Such “first occurrence” data are suspect and open to revision with the discovery of new material. Further, Muller queries several of the identifications that he reports; there is no guarantee that all of the individual reports will stand the test of time. However, the parallelism between the two records suggests that these data are useful, and that the general patterns will hold even if specific cases are found to be in error.

Many of the taxa belong to families known in the fossil record by the Early Eocene (see TABLE 1) and could thus have been members of the boreotropical flora. However, many other taxa sharing the modern eastern Asian–eastern North American distribution belong to families that arose long after the boreotropical flora is assumed to have been broken up by drifting continents and cooling climates. These must have had a geographic history separate from that of the more classic early Tertiary taxa, although they share this modern distribution pattern.

HERBS AND TREES. This pattern of different times of origin of different taxonomic groups has a parallel in the histories of herbaceous and woody plants. Many herbaceous taxa (e.g., members of the Araceae, Araliaceae, Compositae, Cyperaceae, Liliaceae, Polygonaceae, Primulaceae, Ranunculaceae, Rubiaceae, Santalaceae, Umbelliferae) have an eastern Asian–eastern North American distribution.

In general, the paleobotanical literature (e.g., Muller's (1981) data on first appearances, which basically agree with my data on fruits and seeds) tends to emphasize the appearance of herbaceous families in the mid-Tertiary. These herbs are generally assumed to have evolved through neoteny from woody ancestors (Takhtajan, 1976) in response to increasing seasonality in rainfall and/or temperature. Often these herbs were important in the expanding grass-dominated biomes of the time, the prairies and savannas. However, this picture is misleading, because herbs were present before the Miocene and may be presumed to have occupied unstable sites or to have formed forest-floor associations in angiosperm and gymnosperm communities. Evidence for this is the occurrence of individual taxa (e.g., *Ranunculus* L., *Polanisia* Raf.) and even entire groups (e.g., the Monocotyledoneae, which are inherently herbaceous) in early Tertiary floras. Thus, all herbaceous angiosperms sharing an eastern Asian–eastern North American distribution may not have had a similar history. Some may have spread with the boreotropical flora as forest-floor herbs or as early successional colonists of disturbed sites. Others may have evolved in the later Tertiary and spread either by continuous range expansion within the deciduous communities of the Bering or North Atlantic land bridges or by chance long-distance dispersal.

This separation of historical types among herbs is both a complication for paleophytogeographic inquiry and an opportunity to break such a study into component parts. Individual groups will have individual histories, but I suggest that at least four broadly overlapping historical patterns (reflecting, in part, the ecologies of the plants involved) can be predicted for herbs. First would be the plants of the forest-floor association. While some members of this group (particularly those adapted to flowering before leaves of the forest canopy appear in the spring) would be expected to evolve with the diversifying mixed-mesophytic forest of the mid-Tertiary, others were likely present in the early Tertiary. These would belong to lineages with at least a Paleogene fossil record, and they would probably be rhizomatous perennials adapted to stable, low-light environments (see Li, 1952). The long fossil history of monocots (Doyle, 1973) suggests that they would play an important role in this group. Second would be plants of disturbed forest sites. Again, these might belong to lineages with a Paleogene fossil record, but they might be biennials or shorter-lived perennials with good dispersal and other adaptations to the patchy and transient nature of disturbed forest sites. Plants in these groups could also have attained an eastern North American–eastern Asian distribution quite early. The third group, which would include plants adapted to continually disturbed or stressed environments, would comprehend herbs of many different life-histories and would be dominated by groups that evolved in the mid-Tertiary (e.g., Compositae). A fourth and unique group would be composed of aquatic angio-

sperms. Their adaptation to the common, stable but patchy and short-lived habitats of lakes and other bodies of fresh water suits them to a broad distribution. This mode of existence has been present almost since the origin of the angiosperms (Doyle & Hickey, 1976; Hickey & Doyle, 1977), and the inclusion of aquatics in the eastern Asian–eastern North American pattern may predate the boreotropical flora.

These categories are general; variants and intergradations will occur, particularly since members of each category have undoubtedly evolved throughout the Tertiary, although at greater rates during some periods than during others. Further, the fossil record and the biology of individual plants will constrain the success with which these categories can be recognized. For example, *Jeffersonia* Barton, *Podophyllum* L., and *Diphylleia* Michaux (Berberidaceae), and *Dicentra* Borkh. (Papaveraceae) all exemplify the first category of rhizomatous forest-floor herbs that might be expected to trace their eastern Asian–eastern North American distribution to the early Tertiary. However, pollen of Berberidaceae is not known in the fossil record and fruits and seeds appear only in the Late Miocene (TABLE 1), while no record is available for the Papaveraceae. Either the fossil record is incomplete or these taxa moved after the early Tertiary. For the Berberidaceae the fossil record of pollen, fruits, and seeds may be shown to be incomplete since leaves of *Mahonia* Nutt. are known from Late Eocene–earliest Oligocene sediments in the American West (Leopold & MacGinitie, 1972). However, this extension fails to push the family back to the warmest climates of the Early Eocene, possibly indicating that it expanded after the spread of the boreotropical flora.

Although this suggestion of groupings is speculative, it establishes a perspective. More importantly, it emphasizes that herbaceous plants sharing a common distribution pattern in the modern day need not have attained this distribution in the same way or at the same time. The ecology, phylogeny, and fossil record of individual taxa must be studied before an informed hypothesis about the biogeographic history of a group can be made.

BIOGEOGRAPHIC HISTORY AND CLIMATIC REQUIREMENTS. The climate of the past 65 million years has ranged from the widespread, equable conditions of the early Tertiary that brought tropical taxa to far northern latitudes (Reid & Chandler, 1933; Chandler, 1964; Wolfe, 1975) to the glacial maxima of the Pleistocene. The pattern of change from one extreme to the other was not directional and gradual in any but the broadest sense; continued paleoclimatic research (Kennett, 1977; Bucharth, 1978; Wolfe, 1978; Keller, 1983) demonstrates that the overall cooling trend of the Tertiary was marked by fluctuations. The interplay between climatic fluctuations and changing intercontinental geographic connections through the Tertiary has determined the availability of “migration” routes to plants.

The climatic history of the Northern Hemisphere Tertiary commences with temperate (Hickey, 1981b) or cool-paratropical conditions (Wolfe, pers. comm.) in the mid-latitudes from the Cretaceous-Tertiary boundary through the Paleocene. Temperatures warmed, with fluctuations, into the Early and Middle Eocene, supporting tropical vegetation in equable climates at high latitudes,

although perhaps with a simultaneous reduction of average annual equatorial temperatures (Shackleton, 1981). In the Middle to Late Eocene, climates gradually cooled, leading to a sharp decline in the latest Eocene or at the Eocene-Oligocene boundary (Kennett, 1977; Buchardt, 1978; Wolfe, 1978; Collinson *et al.*, 1981). Although we have less knowledge of Oligocene climates, evidence suggests a generally cooler period, with a warming trend beginning in Late Oligocene time and extending into the Miocene. Miocene climates were generally equable and fairly warm, but not as warm as those of the Eocene. More importantly, they were characterized by a series of fluctuations (Kennett, 1977; Wolfe, 1978; Mai, 1980) between warmer and cooler temperatures, leading to increasingly cooler climates in the later Miocene. From the Late Miocene through the Pliocene to the Pleistocene, climates cooled off, with fluctuations, to a situation approximating that of the present day.

Changing climates have had a direct effect upon the evolution and distribution of Tertiary plant communities. In particular, Mai (1964) and Wolfe (1969) both discuss the development of the mixed mesophytic forest as a function of Miocene climatic fluctuations. Szafer (1961), Leopold (1967), and Friis (1975) detail the effect of increasing seasonality in the Late Miocene, Pliocene, and Pleistocene on European plant communities. It is clear from such studies that the climatic tolerances of many angiosperm taxa could not be altered; these taxa either moved via dispersal or became extinct. Others were able to adapt to the cooler, more seasonal climates of the later Tertiary, adding to the growth of deciduous communities (Mai, 1964; Wolfe, 1969). In general, the fossil record suggests that the direction of evolution of tolerance was from paratropical to temperate climates; there is no suggestion that paratropical taxa consistently crossed temperate barriers by evolving temperate forms and then reevolving paratropical ones. We may safely assume that the eastern Asian-eastern North American pattern among evergreen or thermophilic taxa arose at a time when these plants could move directly between the two areas and is not a result of parallel evolution from widespread, deciduous, temperate common ancestors.

The floristic similarity between eastern Asia and eastern North America involves "tropical" evergreen and thermophilic taxa, temperate deciduous taxa, and boreal and alpine taxa. Tropical taxa require no frost, adequate moisture, and sufficient year-round light to support an evergreen physiology. These environmental constraints were met in the Early Eocene when the congruence of warm climates and the availability of the North Atlantic bridges and perhaps the southern margin of the Bering bridge (Wolfe, 1978, in press; Tiffney, 1985) provided a connection between the Old and New worlds. We may assume that evergreen or obligate thermophilic taxa with an eastern Asian-eastern North American pattern in the present day generally attained this distribution as part of the boreotropical flora.

The situation is less clear for temperate taxa with this geographic pattern. I see three possible ways in which such taxa could have achieved this distribution. First, as Hickey has implied (Hickey *et al.*, 1983), temperate elements could have evolved near the early Tertiary North Pole, developing a deciduous habit in response to annual fluctuations in day length. These taxa could have moved

southward with cooling temperatures in the later Eocene, attaining a "boreotropical" distribution in the process. Some taxa certainly followed this route, but the known early Tertiary Arctic floras are species poor and do not account for all of the temperate taxa presently shared between the Old and New World portions of the Northern Hemisphere. Second, as Wolfe (1969, 1977) suggests, these temperate-adapted taxa could have evolved in parallel in the Old and New worlds from thermophilic ancestors that attained their distribution with the Eocene spread of the boreotropical flora. It seems unlikely to me that this could account for the entire temperate floristic similarity of eastern Asia and eastern North America. However, in many cases (e.g., oaks) where there are good tropical relatives of the temperate taxa in the modern day and/or where a transition from a tropical ancestor to a temperate descendant can be demonstrated in the fossil record (see Wolfe, 1969), this is a reasonable supposition. The third possible explanation is that these temperate taxa evolved in post-Eocene time in one portion of the Northern Hemisphere and moved to other regions during the mid-Tertiary, when temperate vegetation was still present at high latitudes (Wolfe, 1972). Such an exchange could have occurred via the Bering land bridge, which was present through the Tertiary and was closed to temperate plants by climatic barriers only in the latest Tertiary or Quaternary. It is also possible that some exchange could have occurred across the post-Eocene North Atlantic by "island hopping" (see, for example, Heie & Friedrich, 1971; McKenna, 1983b), but supporting evidence for this is less clear.

I believe that the similarity in temperate taxa between eastern Asia and eastern North America has arisen through some combination of (at least) these three patterns. Researchers interested in temperate taxa shared between these areas should examine the history and affinities of individual taxa to see if they fit one of these patterns.

Finally, although the fossil record of boreal and alpine taxa is virtually nonexistent, we may assume that many of these plants evolved in the later Tertiary and Quaternary in response to cooling world climate. Particularly since the Bering bridge lay at a high latitude and was functional in the later Tertiary and Quaternary, there is little difficulty in ascribing the similarities of Asian and western North American montane floras to direct exchange. However, workers should be sensitive to the possibility of parallel evolution of montane taxa in the two areas from related temperate ancestors, as well as to long-distance dispersal.

MAJOR HISTORICAL DISTRIBUTION PATTERNS AND EASTERN ASIAN-EASTERN NORTH AMERICAN FLORISTIC SIMILARITY

In the preceding section perspectives and physical variables involved in the origin of the similarity of the floras of eastern Asia and eastern North America were explored. The apparent independent nature of these factors (e.g., climate, geography, evolution) could be expected to predispose me to the view that the history of this floristic pattern involves so many permutations that it would change continuously through time and not be divisible into stages. However,

while the variables are "continuous" in one sense, they are often grouped and form coherent patterns. In particular, climatic variation may be seen as occurring in several "stages" during the Tertiary, and the variables of geography and evolution are not fully independent of climate. Geography may influence climatic change (e.g., moving continents and oceanic currents—Kennett (1977), Berggren (1982)), and climatic change and geography certainly influence evolution. Therefore, one can discern a series of stages in the evolution of the floristic similarity between eastern Asia and eastern North America. These are offered as hypotheses for testing, not as final conclusions destined to replace existing hypotheses or conclusions.

At the outset, it is appropriate to list the variables.

GEOGRAPHY. Two major routes connect the Old and New worlds: the Bering and the North Atlantic land bridges. The former was available throughout the Tertiary, although with occasional breaks enforced by climatic change. The latter involved at least four geographic links, two between North America and Greenland, one between Greenland and Fennoscandia, and one between Greenland and southwestern Europe (McKenna, 1983a, 1983b).

CLIMATES. As detailed above, world climate was cool or, at most, moderately warm at the beginning of the Tertiary. It warmed into the Early Eocene to an Early to mid-Eocene maximum, commenced cooling in the mid-Eocene with a sharp drop in the Late Eocene, remained cool through most of the Oligocene, and then warmed into the Miocene, although not to the degree achieved in the Eocene. A cooling trend began in the Late Miocene and has continued to the present. These general climatic trends were overlain by a secondary pattern of fluctuation that affected the floras of specific times, but not the broad pattern under discussion.

MAJOR PERIODS OF EVOLUTION. Two distinct periods in which modern angiosperm families appeared at an accelerated rate occurred during the Tertiary (see Muller, 1981; Tiffney, 1981, and unpubl. data). From the Cretaceous-Tertiary boundary to the Early Eocene, many modern families appeared. These were largely families dominated by trees. The Late Oligocene and Miocene saw a second diversification, this time largely involving families dominated by herbs. It must be emphasized that, from the Cretaceous to the present, new families were always appearing. The two specific times cited are only times of "increased" rate of family appearance.

POSSIBLE GENERAL PATTERNS

Taking geography, climate, and evolution as the three variables, I suggest that at least five historical patterns contribute to the floristic similarity between eastern Asia and eastern North America.

PRE-TERTIARY. Our knowledge of pre-Tertiary angiosperm evolution and biogeography is limited, but the existence of the Normapolles and *Aquillapollenites* floristic provinces in the later Cretaceous suggests that some Tertiary biogeographic patterns could stem from Cretaceous antecedents. This might be par-

ticularly true of aquatic angiosperms and monocots. I suspect that many conifers (perhaps excluding some Pinaceae, a family that shows modernization concomitant with that of the angiosperms—Miller (1976)) and some bryophytes and pteridophytes may also have attained an eastern Asian–eastern North American distribution at this time.

EARLY EOCENE. The basic components of the boreotropical flora evolved in the Paleogene. The combination of warm climates at high latitudes and the existence of the Bering and North Atlantic land bridges made available the boreal land routes necessary for its spread. I expect that the majority of evergreen taxa presently fitting into the eastern Asian–eastern North American pattern (e.g., Magnoliaceae, Lauraceae, Theaceae) attained their distribution at this time via the North Atlantic bridges. These arborescent taxa were probably accompanied by many herbs of the forest floor or disturbed forest sites. Some deciduous trees may have spread about the hemisphere at this time, perhaps occupying marginal sites in the primarily evergreen boreotropical forest.

LATE EOCENE–OLIGOCENE. As the climates cooled during this period, the deciduous taxa of the polar realms (Hickey *et al.*, 1983) spread southward; some may already have spread to marginal sites earlier in the Eocene. The North Atlantic bridges broke up in the Early Eocene (McKenna, 1983a), cutting off direct movement between Europe and North America. Taxa adapted to cooler, more seasonal sites may have moved via the Bering bridge.

MIOCENE. The Bering bridge remained a viable route, but the temperatures at high latitudes dictated that only temperate deciduous plants could be exchanged between Asia and North America. The North Atlantic land bridges may have existed as a series of island “stepping stones” into the mid-Tertiary and might have permitted the passage of some deciduous taxa. Many deciduous tree lineages evolved during this time (Wolfe, 1969). With regard to the origin of the similarity of the deciduous elements of eastern Asia and eastern North America, it is unclear how many of these evolved in one area and moved via the Bering bridge to the other, and how many evolved in parallel in the two separate areas from common ancestors in the boreotropical flora. This period also saw the evolution of many herbaceous angiosperm groups. Many of these exhibit an eastern Asian–eastern North American distribution, which might have arisen in one of two ways: movement via the Bering bridge by colonization of disturbed sites in the existing forests or development of open communities, or spread by long-distance dispersal, a character common in such plants. I think the latter explanation is less important in view of prevailing wind directions.

LATE TERTIARY–QUATERNARY. With the advent of cold climates in the polar region and on high mountains in the latest Tertiary, it is likely that modern Arctic-alpine forms evolved. The widespread high mountains of Asia and western North America and their point of “meeting” in the northern Pacific provide ample explanation for the movement of these taxa from one area to the other. Some of these taxa may also prove to be derived from common

herbaceous ancestors that spread to occupy an eastern Asian–North American range earlier in time.

OTHER. In any such generalized series of categories, there must be a repository for organisms that do not fit the other classes. Taxa that fit into this category may be unique in their history or may represent another pattern that I have failed to suggest.

EXHORTATION

Investigators working on specific plants with an eastern Asian–eastern North American distribution should attempt to determine which of these patterns (if any) their taxon exhibits. They should seek out the assumed geologic time of origin of that taxon and ascertain its climatic and ecological affinities. From such data it is possible to hypothesize the earliest time at which the taxon attained its present distribution. Such information will enhance the value of research on individual taxa. For example, knowledge of which pattern most closely agrees with the history of a taxon will provide an approximate time of separation of its eastern Asian and its eastern North American members. This in turn permits the estimation of rate—perhaps of karyotypic or chemical differentiation, perhaps of morphological or ecological evolution. Such data also aid the paleontologist to understand past floristic movements and ultimately to assess the validity of the five models suggested above. It should be clear that the study of this pattern on a geographic basis is *not* the province of the paleontologist and phytogeographer alone, but requires knowledge from all associated fields.

SUMMARY

Discussion of Southeast Asia as the cradle or the grave of the modern flora of the Northern Hemisphere, and of angiosperms, is misleading; this area is a giant refugium. However, this implies that another “center of origin” is to be sought. I do not think that such a center exists. I suggest that the antecedent of the modern flora of the Northern Hemisphere (the boreotropical flora of Wolfe) had its origins from several separate sources.

The debate whether plants move in communities or only as individuals is fallacious. Plants disperse as individuals. Plants having similar ecological tolerances generally respond to similar environmental stimuli in a similar manner. The myopic perspective induced by the fossil record makes it likely that, as environmental factors change through geologic time, the paleontological observer will witness apparent movements of groups of plants. The recognition of a “floral migration” is thus reasonable but must always be tempered by the knowledge of the underlying biological pattern of the dispersal of individuals.

The early Tertiary boreotropical flora developed in a unique geographic situation involving two sets of land bridges (Bering and North Atlantic) existing at different latitudes in a time of warm and equable climates. This permitted a free movement of newly evolved taxa and the development of a hemispheric flora. No evidence exists for monolithic “geofloras” in the classic sense. The

boreotropical flora was not homogeneous; local differentiation existed. Individual plant migrations resulted in most taxa occurring in some portion of the range of the boreotropical flora at some time, but few taxa occurring in all of the range of the flora all of the time.

Taxa exhibiting the eastern Asian–eastern North American distribution include forms that evolved in both the early and later portions of the Tertiary. The modern similarity of the two areas is the product of more than one biogeographic event.

The perception of herbaceous angiosperms as primarily a phenomenon of the mid-Tertiary is wrong. Aquatic herbs and monocotyledons have existed almost since the origin of the angiosperms. Forest-floor herbs existed in the Early Eocene boreotropical flora. While the mid-Tertiary did witness a major diversification of herbaceous taxa adapted to disturbed sites, these were not the first, nor the only important, angiosperm herbs.

The modern eastern Asian–eastern North American pattern of distribution did not arise through a single historical event but is the result of a layering of many events. Some aspects of the similarity may trace their roots to pre-Tertiary times. A large number of taxa, many evergreen, achieved this distribution in the warm climates of the Early and Middle Eocene. Deciduous taxa may have accompanied these floras, moved later in the Tertiary during times of cooler climate, or evolved in parallel from evergreen ancestors inhabiting both areas. Herbaceous forms may have achieved the distribution at various times, depending on their particular ecological affinities.

All of these observations complicate our understanding of the origin of this biogeographic pattern and the mechanisms underlying it. However, if the question is broken down into component parts, it may be easier to address the overall pattern.

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LITERATURE CITED

- AXELROD, D. I. 1966. The evolution of flowering plants. Pp. 227–305 *in* S. TAX, ed., *Evolution after Darwin*. Vol. 1. Univ. Chicago Press, Chicago.
- BERGGREN, W. A. 1982. Role of ocean gateways in climate changes. *Acta Univ. Stockholm* 37: 9–20.

- BOUFFORD, D. E., & S. A. SPONGBERG. 1983. Eastern Asian-eastern North American phytogeographical relationships—a history from the time of Linnaeus to the twentieth century. *Ann. Missouri Bot. Gard.* **70**: 423–439.
- BUCHARDT, B. 1978. Oxygen isotope palaeotemperatures from the Tertiary period in the North Sea area. *Nature* **275**: 121–123.
- CARLQUIST, S. 1974. *Island biology*. ix + 660 pp. Columbia Univ. Press, New York.
- CHANDLER, M. E. J. 1964. The lower Tertiary floras of southern England. IV. A summary and survey of findings in light of recent botanical observations. xii + 151 pp. British Museum (Natural History), London.
- CHANEY, R. W. 1947. Tertiary centers and migration routes. *Ecol. Monogr.* **17**: 139–148.
- CLEMENTS, F. E. 1916. *Plant succession. An analysis of the development of vegetation.* Publ. Carnegie Inst. Wash. **242**: 1–512.
- . 1928. *Plant succession and indicators*. xvi + 453 pp. H. W. Wilson Co., New York.
- COLLINSON, M. E., K. FOWLER, & M. C. BOULTER. 1981. Floristic changes indicate a cooling climate in the Eocene of southern England. *Nature* **291**: 315–317.
- CONSTANCE, L. 1972. Patterns in the distribution of Japanese-American Umbelliferae. Pp. 93–99 in A. GRAHAM, ed., *Floristics and paleofloristics of Asia and eastern North America*. Elsevier Publ. Co., Amsterdam.
- DARWIN, C. 1859. *On the origin of species by means of natural selection*. ix + 490 pp. J. Murray, London.
- DAVIS, M. B. 1976. Pleistocene biogeography of temperate deciduous forests. *Geosci. & Man* **13**: 13–26.
- . 1981. Quaternary history and the stability of forest communities. Pp. 132–153 in D. C. WEST, H. H. SHUGART, & D. B. BOTKIN, ed., *Forest succession: concepts and application*. Springer-Verlag, New York.
- DOYLE, J. A. 1973. Fossil evidence on the early evolution of the monocotyledons. *Quart. Rev. Biol.* **48**: 399–413.
- & L. J. HICKEY. 1976. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. Pp. 139–206 in C. B. BECK, ed., *Origin and early evolution of angiosperms*. Columbia Univ. Press, New York.
- EYSINGA, F. W. D. VAN. 1975. *Geological time table*. ed. 3. Elsevier Scientific Publ. Co., Amsterdam.
- FRIIS, E.-M. 1975. Climatic implications of microcarpological analyses of the Miocene Fæstherholt flora, Denmark. *Bull. Geol. Soc. Denmark* **24**: 179–191.
- GLEASON, H. A. 1926. The individualistic concept of the plant association. *Bull. Torrey Bot. Club* **53**: 7–26.
- GRAHAM, A. 1972a. Outline of the origin and historical recognition of floristic affinities between Asia and eastern North America. Pp. 1–16 in A. GRAHAM, ed., *Floristics and paleofloristics of Asia and eastern North America*. Elsevier Publ. Co., Amsterdam.
- , ed. 1972b. *Floristics and paleofloristics of Asia and eastern North America*. xii + 278 pp. Elsevier Publ. Co., Amsterdam.
- GRAY, A. 1840. Dr. Siebold, *Flora Japonica*; sectio prima, Plantas ornatui vel usui inservientes; digessit Dr. J. G. Zuccarini: fasc. 1–10, fol. (Review). *Amer. J. Sci. Arts* **39**: 175, 176.
- . 1859. Diagnostic characters of phanerogamous plants, collected in Japan by Charles Wright, botanist of the U. S. North Pacific Exploring Expedition, with observations upon the relations of the Japanese flora to that of North America, and of other parts of the northern Temperate Zone. *Mem. Amer. Acad. Arts Sci.* n.s. **6**: 377–453.
- . 1878. *Forest geography and archaeology. A lecture delivered before the Harvard University Natural History Society.* *Amer. J. Sci. Arts*, III. **16**: 85–94, 183–196.

- GUO, S. 1980. Late Cretaceous and Eocene floral provinces. 9 pp. Privately published for distribution at the first conference of the International Organization of Paleobotany, Reading, England, 1980.
- HEIE, O. E., & W. L. FRIEDRICH. 1971. A fossil specimen of the North American hickory aphid (*Longistigma caryae* Harris), found in Tertiary deposits in Iceland. *Ent. Scand.* 2: 74–80.
- HICKEY, L. J. 1973. Classification of the architecture of dicotyledonous leaves. *Amer. J. Bot.* 60: 17–33.
- . 1981a. Late Cretaceous and Tertiary vegetation and climate of the Arctic. (Abstract.) XIII Int. Bot. Congr., p. 197.
- . 1981b. Land plant evidence compatible with gradual, not catastrophic, change at the end of the Cretaceous. *Nature* 292: 529–531.
- & J. A. DOYLE. 1977. Early Cretaceous fossil evidence for angiosperm evolution. *Bot. Rev. (Lancaster)* 43: 3–104.
- , R. M. WEST, M. R. DAWSON, & D. K. CHOI. 1983. Arctic terrestrial biota: paleomagnetic evidence of age disparity with mid-northern latitudes during the Late Cretaceous and early Tertiary. *Science* 221: 1153–1156.
- & J. A. WOLFE. 1975. The bases of angiosperm phylogeny: vegetative morphology. *Ann. Missouri Bot. Gard.* 62: 538–589.
- HSÜ, J. 1983. Late Cretaceous and Cenozoic vegetation in China, emphasizing their connections with North America. *Ann. Missouri Bot. Gard.* 70: 490–508.
- ILTIS, H. H. 1982. Long-distance dispersal (LDD) within the “Arcto-Tertiary” Geoflora: eastern North America and eastern Asia as climatically equivalent floristic archipelagoes. Biogeographical relationships between temperate eastern Asia and temperate eastern North America. (Abstract.) 29th Ann. Syst. Symp., Missouri Bot. Gard., pp. 20, 21.
- . 1983. Biogeographical relationships between temperate eastern Asia and temperate eastern North America. Pp. 49–51 in *Proceedings of the U.S.–Japan science seminar on the origin of the East Asian and North American floras from Arctotertiary precursors*. United States–Japan Cooperative Science Program.
- KELLER, G. 1983. Paleoclimatic analysis of Middle Eocene through Oligocene planktic foraminiferal faunas. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 43: 73–94.
- KENNETT, J. P. 1977. Cenozoic evolution of Antarctic glaciation, the Circum-Antarctic Ocean, and their impact on global paleoceanography. *J. Geophys. Res.* 82: 3843–3860.
- KOYAMA, H. 1983. Phytogeography of some genera of Compositae confined to Japan and eastern North America. Pp. 21–33 in *Proceedings of the U.S.–Japan science seminar on the origin of the East Asian and North American floras from Arctotertiary precursors*. United States–Japan Cooperative Science Program.
- KOYAMA, T. 1983. Cyperaceae with eastern Asiatic and North American disjunct distribution. Pp. 43, 44 in *Proceedings of the U.S.–Japan science seminar on the origin of the East Asian and North American floras from Arctotertiary precursors*. United States–Japan Cooperative Science Program.
- LEOPOLD, E. B. 1967. Late Cenozoic patterns of plant extinction. Pp. 203–246 in P. S. MARTIN & H. E. WRIGHT, eds., *Pleistocene extinctions*. Yale Univ. Press, New Haven.
- & H. D. MACGINITIE. 1972. Development and affinities of Tertiary floras in the Rocky Mountains. Pp. 147–200 in A. GRAHAM, ed., *Floristics and paleofloristics of Asia and eastern North America*. Elsevier Publ. Co., Amsterdam.
- LI, C. K., & S. Y. TING. In press. The Paleogene mammals of China—the faunas, the systematic and geological distribution, bibliography, and index. *Bull. Carnegie Mus. Nat. Hist.*
- LI, H. L. 1952. Floristic relationships between eastern Asia and eastern North America. *Trans. Amer. Philos. Soc. n.s.* 42: 371–429.
- . 1972. East Asia–eastern North America species-pairs in wide-ranging genera.

- Pp. 65–78 in A. GRAHAM, ed., *Floristics and paleofloristics of Asia and eastern North America*. Elsevier Publ. Co., Amsterdam.
- MAI, D. H. 1964. Die Mastixioideen-Floren im Tertiär der Oberlausitz. *Paläontol. Abh., Abt. B, Paläobot.* 2: 1–192.
- . 1976. Eozäne Floren des Geiseltales. *Abh. Zentr. Geol. Inst.* 26: 93–149.
- . 1980. Change of climate and biostratigraphy in the continental younger Tertiary of boreal province. *Giorn. Geol. II.* 35: 85–90.
- & H. WALTHER. 1978. Die Floren der Haselbacher Serie im Weisselster-Becken (Bezirk Leipzig, DDR). *Abh. Staatl. Mus. Mineral. Geol. Dresden* 28: 1–200.
- MANCHESTER, S. R. 1981a. Fossil plants of the Eocene Clarno Nut Beds. *Oregon Geol.* 43: 75–81.
- . 1981b. Fossil history of the Juglandaceae. vii + 209 pp. Unpubl. Ph.D. Thesis, Indiana Univ., Bloomington.
- . 1983. Fruits and seeds of *Tapiscia* (Staphyleaceae) from the Middle Eocene of Oregon. (Abstract.) *Amer. J. Bot.* 70(5, part 2): 74.
- McKENNA, M. C. 1983a. Cenozoic paleogeography of North Atlantic land bridges. Pp. 351–399 in M. H. P. BOTT, S. SAXOV, M. TALWANI, & J. THIEDE, eds., *Structure and development of the Greenland-Scotland ridge*. Plenum Press, New York.
- . 1983b. Holoarctic land mass rearrangement, cosmic events, and Cenozoic terrestrial organisms. *Ann. Missouri Bot. Gard.* 70: 459–489.
- MILLER, C. N. 1976. Early evolution in the Pinaceae. *Rev. Palaeobot. Palynol.* 21: 101–117.
- MULLER, J. 1968. Palynology of the Pedawan and Plateau Sandstone formations (Cretaceous–Eocene) in Sarawak, Malaysia. *Micropaleontology* 14: 1–37.
- . 1970. Palynological evidence on early differentiation of angiosperms. *Biol. Rev. Cambridge Philos. Soc.* 45: 417–450.
- . 1981. Fossil pollen records of extant angiosperms. *Bot. Rev. (Lancaster)* 47: 1–142.
- PALAMAREV, E. 1973. Die Eozäne Flora des Burgas-Beckens. (In Bulgarian, with German summary.) *Izv. Bot. Inst. (Sofia)* 24: 75–124.
- RAVEN, P. H., & D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61: 539–673.
- REID, E. M., & M. E. J. CHANDLER. 1933. *The London Clay flora*. viii + 561 pp. British Museum (Natural History), London.
- SCOTT, R. A. 1954. Fossil fruits and seeds from the Eocene Clarno formation of Oregon. *Palaeontographica, Abt. B., Paläophytol.* 96: 66–97.
- SHACKLETON, N. J. 1981. Cenozoic climatic variability. (Abstract.) *Terra Cognita* 1981: 109.
- SHARP, A. J. 1972. The possible significance of some exotic distributions of plants occurring in Japan and/or North America. Pp. 61–64 in A. GRAHAM, ed., *Floristics and paleofloristics of Asia and eastern North America*. Elsevier Publ. Co., Amsterdam.
- SHIMIZU, T. 1983. Distributional patterns of U.S.–Japan elements, with special references to the alpine and the frigid zone. Pp. 35–42 in *Proceedings of the U.S.–Japan science seminar on the origin of the East Asian and North American floras from Arctotertiary precursors*. United States–Japan Cooperative Science Program.
- SMITH, A. C. 1970. *The Pacific as a key to flowering plant history*. 28 pp. University of Hawaii, Harold L. Lyon Arboretum Lecture Number 1.
- SRIVASTAVA, S. K. 1981. Evolution of Upper Cretaceous phytogeoprovinces and their pollen flora. *Rev. Palaeobot. Palynol.* 35: 155–173.
- SZAFER, W. 1961. Miocene flora from Stare Gliwice in Upper Silesia. *Prace Inst. Geol.* 33: 1–205.
- TAKHTAJAN, A. 1969. *Flowering plants. Origin and dispersal*. x + 310 pp. Smithsonian Inst. Press, Washington, D. C.
- . 1976. Neoteny and the origin of the flowering plants. Pp. 207–219 in C. B.

- BECK, ed., Origin and early evolution of angiosperms. Columbia Univ. Press, New York.
- TAMURA, M. 1983. Distribution and differentiation of some ranunculaceous genera in East Asia and North America. Pp. 9–18 in Proceedings of the U.S.–Japan science seminar on the origin of the East Asian and North American floras from Arctotertiary precursors. United States–Japan Cooperative Science Program.
- THORNE, R. F. 1972. Major disjunctions in the geographic ranges of seed plants. Quart. Rev. Biol. **47**: 365–411.
- TIFFNEY, B. H. 1981. Diversity and major events in the evolution of land plants. Pp. 193–230 in K. J. NIKLAS, ed., Paleobotany, paleoecology and evolution. Vol. 2. Praeger Press, New York.
- . 1985. The Eocene North Atlantic land bridge and its importance in Tertiary and modern phytogeography of the Northern Hemisphere. J. Arnold Arbor. **66**: in press.
- . In press. Seed size, dispersal syndromes and the rise of the angiosperms. Ann. Missouri Bot. Gard.
- TRAVERSE, A. 1955. Pollen analysis of the Brandon Lignite of Vermont. U. S. Dept. Int., Bur. Mines, Rep. Investig. **5151**: 1–107.
- UTECH, F. H. 1983. Vascular floral anatomy of *Japonolirion osense* Nakai (Liliaceae) and its tribal relationship. Pp. 81–84 in Proceedings of the U.S.–Japan science seminar on the origin of the East Asian and North American floras from Arctotertiary precursors. United States–Japan Cooperative Science Program.
- VINOGRADOV, A. P. 1967–1968. Lithological-paleogeographic atlas of U.S.S.R. Vol. 4. Paleogene, Neogene and Quaternary. Izdat. Nauka, Leningrad.
- WADA, K., & M. IHARA. 1983. The application of protein sequence analyses to bio-systematics. Pp. 103–110 in Proceedings of the U.S.–Japan science seminar on the origin of the East Asian and North American floras from Arctotertiary precursors. United States–Japan Cooperative Science Program.
- WANG, C. W. 1961. The forests of China, with a survey of grassland and desert vegetation. Publ. Maria Moors Cabot Found. Bot. Res. **5**: 1–313. Cambridge, Massachusetts.
- WHITTAKER, R. H. 1967. Gradient analysis of vegetation. Biol. Rev. Cambridge Philos. Soc. **42**: 207–264.
- WOLFE, J. A. 1969. Neogene floristic and vegetational history of the Pacific Northwest. Madroño **20**: 83–110.
- . 1972. An interpretation of Alaskan Tertiary floras. Pp. 201–233 in A. GRAHAM, ed., Floristics and paleofloristics of Asia and eastern North America. Elsevier Publ. Co., Amsterdam.
- . 1975. Some aspects of plant geography of the Northern Hemisphere during the Late Cretaceous and Tertiary. Ann. Missouri Bot. Gard. **62**: 264–279.
- . 1977. Paleogene floras from the Gulf of Alaska region. U. S. Geol. Surv. Prof. Pap. **997**: 1–108.
- . 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. Amer. Sci. **66**: 694–703.
- . In press. The relative distribution of major vegetational types during the Tertiary. Proc. Amer. Geol. Union Chapman Conference.

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